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THE ORIGIN OF THE BRILLE IN *CROTALUS*
CONFLUENTUS LUTOSUS (GREAT BASIN
RATTLESNAKE)*

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INTRODUCTION

For over a century zoologists have regarded the transparent outer covering of the eyes of snakes as corresponding to the eyelids in other vertebrates. This covering is known as the "spectacle" or "Brille." Cloquet,¹ in 1821, recorded the first description of the Brille and the proper interpretation of it. A few years later I. Müller² observed the same organ in geckoes. In 1888 Ficalbi³ reported on its histologic structure, and in 1904 Carpi⁴ and Crevatin⁵ described the innervation of the Brille. Research work on its development is recorded by Rathke⁶ as early as 1839 in his embryology of the European viper. In 1890 Seiler⁷ published a study of the embryology of conjunctival sacs in which he discussed the development and structure of the Brille in *Natrix natrix*.

In 1933 H. Schwarz-Karsten⁸ reported on the development and structure of the Brille in snakes and lizards, and on the anatomy of their tear ducts. This article appeared after most of my material for a study of the development of the Brille in *Crotalus confluentus lutosus* had been assembled and many embryologic preparations had been made. Schwarz-

* Candidate's thesis for membership accepted by the Committee on Theses.

Karsten's findings in *Natrix natrix* have been confirmed, and my work on the origin of the Brille in the rattlesnake has been continued.

THEORIES AS TO THE HOMOLOGIES OF THE BRILLE

Many theories have been advanced as to the probable origin of the Brille.

Giovanni Ovio⁹ states: "In snakes, indeed, the eye is constantly covered by the lower eyelid; the upper scarcely reaches the border of the orbit. Due to the fact that it is placed before the cornea one calls it by the name 'lunette' or 'Brille.'"

L. Plate¹⁰ makes the following statement: "So far, the possibility that the Brille of the reptiles may arise like that of many fishes and amphibian larvae from a splitting of the cornea has not been tested."

Hoffmann,¹¹ in Brönn's "Klassen und Ordnungen des Thier-Reichs," states that the transparent eyelid of serpents is divided into two layers with a lymphatic space between.

Fabricius was of the opinion that the Brille was formed from the cornea by being delaminated off, and that this "proved" the cutaneous nature of the corneas of all vertebrates.

The problem of the spectacle or Brille of snakes is discussed in many zoological writings. Plate raises the question as to whether the Brille originates from the eyelids or from the nictitating membrane. The supporters of the "nictitans theory," originally advanced by Gegenbaur, point to the very prominent and well-developed Harderian gland (the gland of the nictitating membrane), and, in contrast, to the fact that the normal lacrimal glands are absent or, when present, are very poorly developed.

Rochon-Duvigneaud^{12, 13} gives a most complete study of the eyes of reptiles, and firmly established the palpebral nature of the ophidian spectacle and the corneal origin of the

one present in most teleosts. He does not accept, however, the possible origin of the ophidian spectacle from the nictitans, and does not conclude whether the lower eyelid alone or both upper and lower eyelids have contributed to form the Brille. Furthermore, he maintains, with truth, that only embryologic study can determine its origin.

MATERIAL AND METHODS

It was quite difficult to obtain rattlesnake embryos in the proper stages of development. Many adult specimens of rattlesnakes were secured on a personal trip to a "den" located in the adobe bank of a dry river in a desert 200 miles south of Salt Lake City. Contrary to the general belief that snakes do not breed in captivity, embryos were obtained after the snakes had been in confinement for eleven months. Additional specimens were obtained from a den located near Fort Collins, Colorado. Mr. L. M. Klauber, Director of the Natural History Museum, Balboa Park, San Diego, California, generously furnished embryos from his collection. The Museum of Vertebrate Zoology, University of California, also contributed material for study. For comparison, *Natrix natrix* embryos were purchased from the Southern Biological Supply Company, of New Orleans.

Bouin's and Carnoy's fluids were found to be most satisfactory for preserving the specimens, as they caused little shrinkage of the tissues. Embryos fixed in 5 per cent. formalin usually showed the Brille and cornea collapsed.

The entire head of the embryo was embedded by the hot celloidin method (Walls,¹⁵ 1932). Serial sections (15 microns) were made in both the vertical and the horizontal planes. In some of the older embryos decalcification with 3 per cent. hydrochloric acid solution was necessary. Considerable difficulty was experienced in cutting thin sections of the horny adult Brille. Hematoxylin and eosin were the principal staining reagents used.

THE RATTLESNAKE EYE

The eye of the rattlesnake (*Crotalus confluentus lutosus*) is located at the junction of the anterior one-fourth and posterior three-fourths of its head, beneath a somewhat firm, projecting supra-ocular scale (fig. 1). This oval scale extends laterally a little beyond the surface of the Brille. In addition to protecting the Brille from mechanical injury, it may also serve as a shade for the vertically slit pupil directly beneath it. In the region of the eye the skin dips down over the margin of the bony orbit from all sides and is attached to the posterior half of the eyeball. The anterior margin of the skin becomes thin and clear as it extends forward, completely encasing the cornea with a transparent convex shield, the Brille. Thus the Brille forms the external wall of the closed conjunctival sac. This sac is lined with epithelium and filled with fluid (fig. 2).

The superficial layer of skin extending from the margin of the orbit to the Brille is extremely thin and pliable. It lies in a number of folds around the base of the Brille, producing a circular recess or cuff formation. These folds are covered with large epithelial cells. At the base of the Brille the layer becomes a transparent, cellophane-like insensible, protective covering (epidermoid) of the entire Brille. This superficial epithelium is cast off as a part of the exuvia (snake's skin), which is usually shed two or three times each year. Just before moulting a milky, albuminous fluid is formed between this external layer and the remainder of the Brille. At this time the eye presents a whitish, opaque appearance, leading to the popular belief that the snake is temporarily blind.

THE HISTOLOGIC STRUCTURE OF THE BRILLE

The histologic structure of the Brille has been described by Cloquet, Ficalbi, and, more recently, by Carpi, Crevatin, and H. Schwarz-Karsten. These investigators describe the Brille as consisting of three layers: an external one, termed

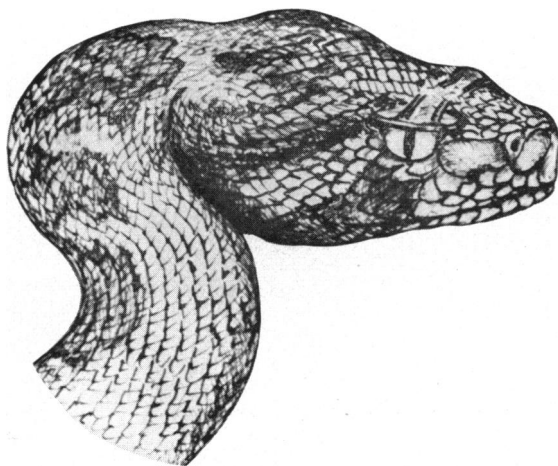


Fig. 1.—*Crotalus confluentus lutosus* (Great Basin Rattlesnake).

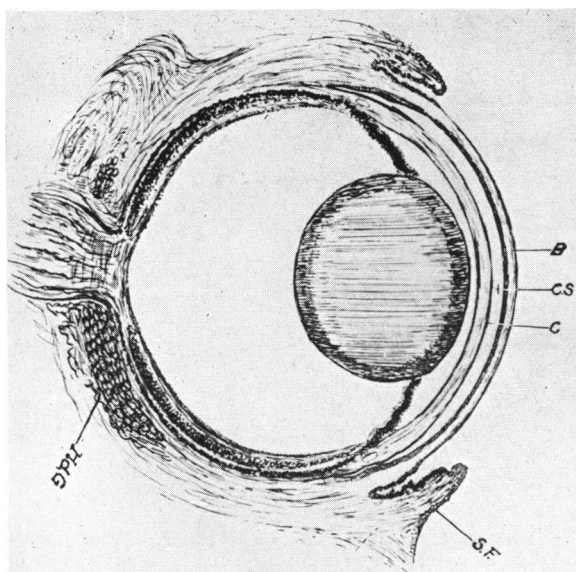


Fig. 2.—Cross-section of eyeball of *Crotalus confluentus lutosus*: *B*, Brille; *C*, cornea; *C.S.*, conjunctival sac; *S.F.*, skin fold; *Hd.G.*, Harderian gland.

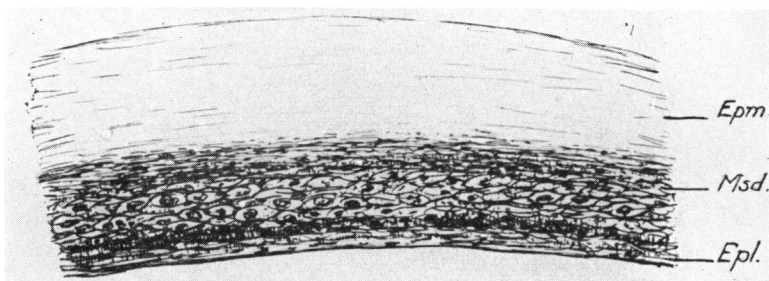


Fig. 3.—Brille—*Crotalus confluentus lutosus*: *Epm*, epidermoid; *Msd.*, mesoderm; *Epl.*, epithelial lining.



Fig. 4.—Head, 5.2 mm. long.



Fig. 5.—Head, 6 mm. long.

Embryos of *Lacerta agilis* (after Schwarz-Karsten).

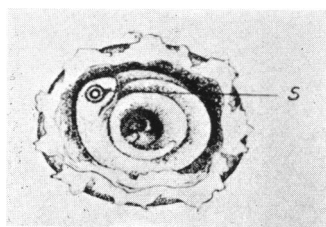


Fig. 6.—Embryo of *Crotalus confluentus lutosus* in egg membranes (normal size). *S*, Lacrimal sulcus.

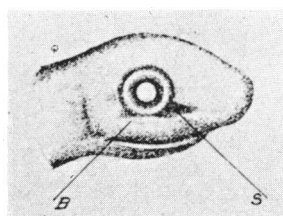


Fig. 7.—Head of embryo of *Crotalus confluentus lutosus*: *B*, Anlage of Brille; *S*, lacrimal sulcus. ($\times 4.25$.)

the epidermoid, which is a continuation of the epidermis; the middle layer, or mesoderm, which is a modification of the corium; and a third or inner layer, which is a continuation of the epithelial layer lining the conjunctival sac. Figure 3 shows a cross-section of the adult Brille in *Crotalus confluentus lutosus*.

The epidermoid comprises about one-half the thickness of the Brille. It is composed of two layers: an outer, lightly staining, somewhat homogeneous horny tissue termed the stratum corneum, and an inner layer that takes a deeper stain and has more visible structure than the outer layer. The portion of the inner layer directly in contact with the stratum corneum is quite compact, and is formed as the result of the germinative basal epithelial cells becoming more elongated and stratified preparatory to the formation of a new stratum corneum to replace the old one when the latter is cast off.

The mesoderm lies directly beneath the epidermoid, and is composed of cells and fibers which are formed into lamellae. Between the lamellae are a few flat connective-tissue cells and an occasional capillary. The inner side of the mesoderm is covered with the same stratified epithelium that lines the entire conjunctival sac.

EMBRYOLOGY OF THE BRILLE

The development of the Brille or spectacle seen in snakes and some other reptiles can best be understood by first considering the formation of the eyelids in reptiles that possess them in mobile form. Schwarz-Karsten has described the development in *Lacerta agilis*. In an embryo head 5.2 mm. long (fig. 4) he found a large eyeball whose entire circumference was encircled by a narrow, circular skin fold. This skin fold originates from the parts of the head closest to the globe. It has two surfaces, one external and the other facing the eyeball. The free edge of the fold forms the margin of an opening, the anlage of the palpebral fissure, which at first is

almost circular. In later stages it advances from all sides, but more rapidly from above and below (fig. 5 shows a head 6 mm. long), until the superior and inferior margins approximate each other. Thus the circular fold of embryonic skin surrounding the globe develops into the upper and lower eyelids, with their commissures and horizontally disposed palpebral fissure.

The first sign of the Brille in the snake is the appearance of a swelling or thickening of the tissue beneath the eyeball in the region of the upper jaw (figs. 7 and 8). This was found in an embryo in which the head measured 4 mm. in length, the globe being 1 mm. in diameter. It will be noted that there is a double row of epithelial cells at the junction of the anlage of the Brille and the cornea preparatory to the separation of the lower lid contribution. This process begins while the cornea and retina are still in their early embryonic state. There is no evidence of the Brille forming above the eyeball in this stage. In a slightly older embryo—one in which the head is 4.5 mm. long—the thickened tissue beneath the globe has pushed forward and is separated from the primitive corneal tissue (fig. 9). Concurrently a swelling is forming above the eyeball, but it is not nearly so far advanced as the lower one. This superior portion of the Brille anlage appears at the time when the anterior portion of the embryonic retina is becoming thin preparatory to the formation of the pars iridis retinae. A few pigment cells are being deposited in the uveal tract, and many optic nerve fibers have decussated at the optic chiasm, to continue their course to the cerebrum.

The pad-like anlagen continue to grow until their ends meet, surrounding the margin of the orbit as a circular skin fold. At this stage of development the early Brille greatly resembles the beginning lid-formation found by Schwarzkarsten in *Lacerta agilis* (figs. 4 and 5). The only break in the circumference is an indentation or groove-like formation, the sulcus lacrimalis, situated between the upper jaw and the

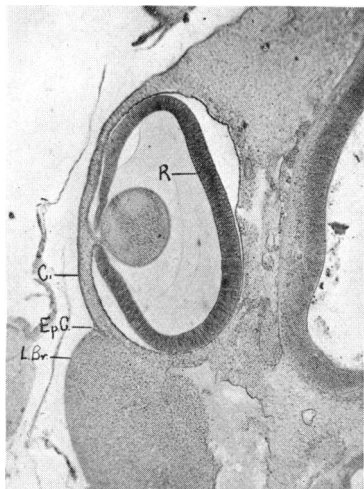


Fig. 8.—Early embryo showing anlage of inferior margin of Brille, *L.Br.*, cornea, *C*, and retina, *R*, are embryonic; *Ep.C.*, separation line of epithelial cells. Head, 4 mm. long. ($\times 33$.)

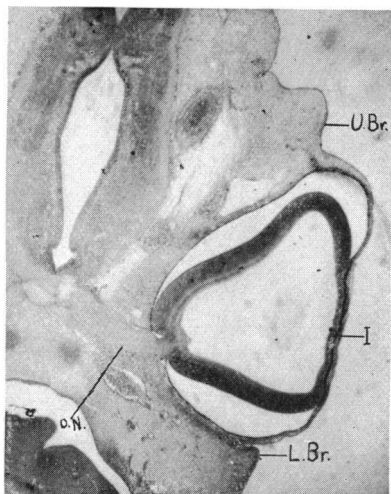


Fig. 9.—Stage showing lower lid contribution, *L.Br.*, separating from cornea, *C*; *U.Br.*, beginning of upper lid contribution. Embryonic retina is becoming thin, to form pars iridis retinae, *I*. Optic nerves, *O.N.*, decussate and fibers ascend along cerebrum. Head 4.5 mm. long. ($\times 24$.)

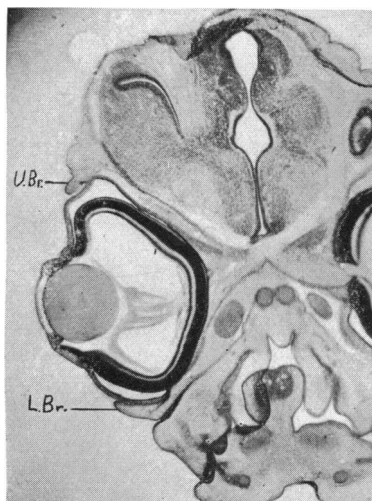


Fig. 10.—Later stage showing increased growth of both lower, *L.Br.*, and upper, *U.Br.*, portions. (Lower grows more rapidly than upper.) (Note the optic chiasm which shows well here.) Head 5 mm. long. ($\times 20$.)

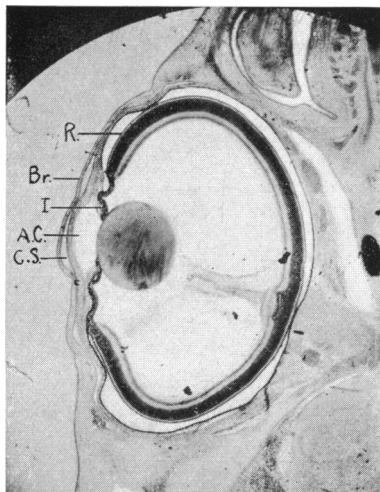


Fig. 11.—Brille lips have united, *Br.*, forming closed subconjunctival sac, *C.S.* Anterior chamber, *A.C.*; iris, *I*; retina, *R*. Head 6 mm. long. ($\times 25$.)

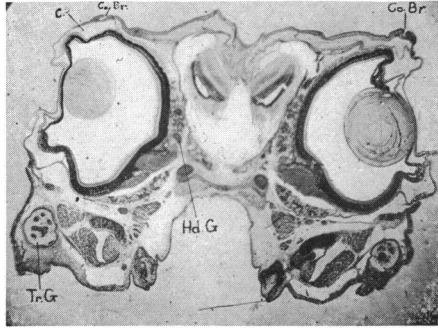


Fig. 12.—Showing location and process of coalescence of Brille lips, *Co.Br.*, near upper fornix of culdesac, *C.S.* Note Harderian gland, *Hd.G.*, in orbit, and atrophic tear gland, *Tr.G.* ($\times 20$.)

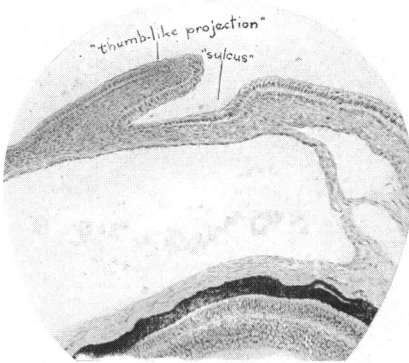


Fig. 13.—($\times 400$.)

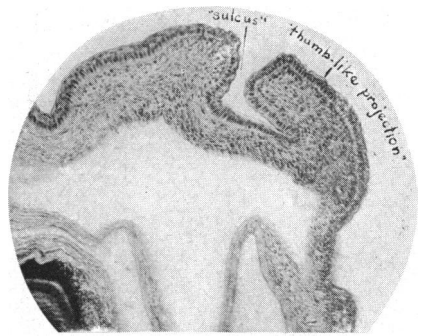


Fig. 14.—($\times 450$.)

Fig. 13 and Fig. 14.—Showing coalescence of Brille in right and left eyes respectively.

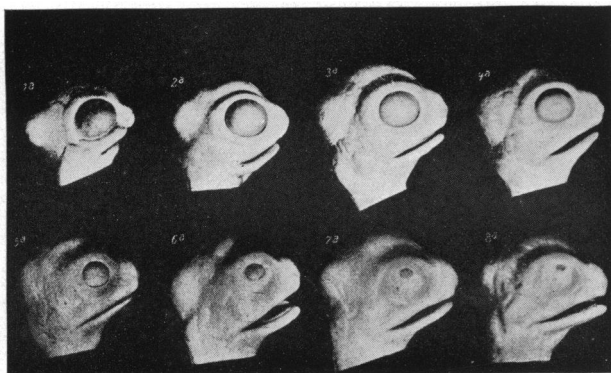


Fig. 15.—Embryos of *Natrix natrix*, showing development of Brille (after Schwarz-Karsten).



Fig. 16.—Horizontal cross-section near end of sulcus showing closing of Brille. *Co.Br.*, Coalescence of Brille lips. (Note tip of crystalline lens, *C.L.*, in same plane as end of sulcus.) ($\times 20$.)

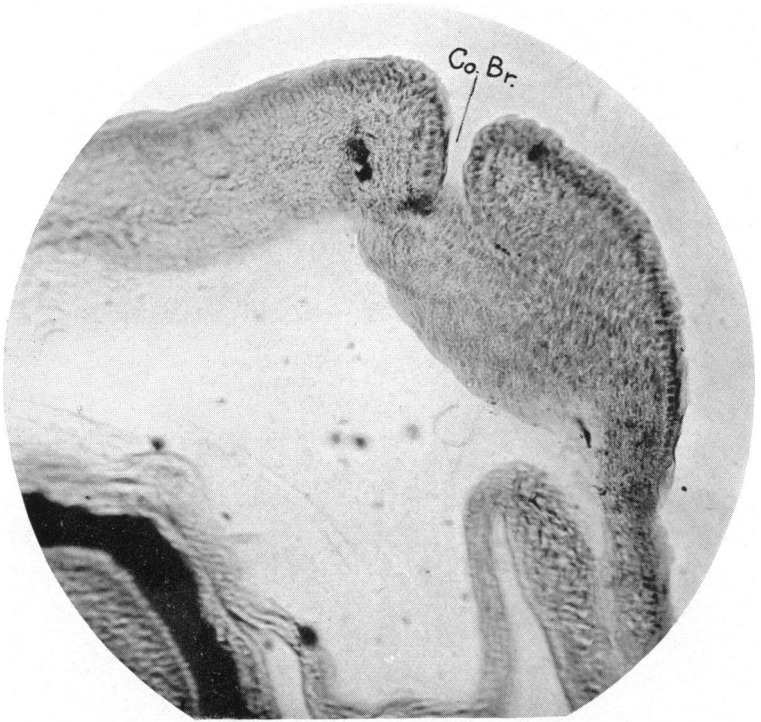


Fig. 17.—V-shaped end of sulcus of left eye seen in figure 16. *Co.Br.*, Coalescence of Brille lips. ($\times 450$.)

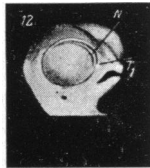


Fig. 18.—Head of an embryo chick showing nictitans, *N*. Anlage of tear duct, *T*. (After Schwarz-Karsten.)

external nasal process (figs. 6 and 7). Schwarz-Karsten states that in the portion of the lacrimal sulcus closest to the eye a solid epithelial prop dips down into the tissue and forms the first anlage of the lacrimal duct.

In the rattlesnake the circular skin fold, which is thicker above and thinner below, grows in from all sides, gradually encasing the cornea (fig. 10). The section from the upper jaw corresponding to the lower lid grows more rapidly and is thinner than the opposing part from above the globe. As the margins of these folds push toward each other the opening which they enclose becomes elliptic. Due to the more rapid growth of the lower lid this elliptic opening is carried upward and grows smaller until it finally closes as a fissure approximately opposite the upper margin of the orbit and near the upper fornix of the culdesac (figs. 11 and 12). From this description it will be seen that the outward appearance of the final closure of the Brille in the rattlesnake differs markedly from that in *Natrix* (fig. 15). In the former the final opening is a fissure, located in a higher plane than the circular closure described by Schwarz-Karsten in *Natrix*.

Coincident with the completion of the Brille the mesoderm is forming the stroma of the pigmented iris and the retina is differentiating into most of the layers seen in the adult (fig. 11).

The exact method of closure of the margins of the transitory aperture in the Brille could not be determined, owing to a lack of sufficient material during the critical stages.

Schwarz-Karsten states that the free edges of the Brille, just before they grow together, surround a funnel-shaped space the narrow opening of which points outward, whereas its wide aperture is in the conjunctiva directed toward the globe. This investigator was unable to determine the method of final closure of the conjunctival opening.

In the rattlesnake the closure of the Brille is different. Instead of forming a round funnel the outer end of which is the first to heal, it apparently closes to a fissure-like forma-

tion. The inner lips of the fissure close first, and their point of coalescence is covered by conjunctival epithelium before the external surface is closed (figs. 13 and 14). This fissure-like closure is approximately as long as the diameter of the crystalline lens, since all sections showing the closure also contain portions of the lens. Each end of the fissure forms a small V-shaped depression (figs. 16 and 17). As the center of its sulcus is approached the external surface of the lower lid contribution appears to be longer, assuming a thumb-like formation, as may be seen in figure 13. Opposite this projection and approximately of the same length, there is a depression or notch in the Brille. The entire sulcus is lined with inflected epithelium. When the closure has finally taken place, one can assume that the thumb-like projection will fit neatly into the notch and eventually be completely coalesced. Sections of the adult Brille were carefully examined for evidence of the line of coalescence, but none could be found.

The Brille is thickest at the point of abolition of its transitory aperture, and gradually becomes thinner toward its center, due to the fact that the basal cells grow longer and thinner. As the opposite, inferior margin is approached it again becomes thicker (fig. 12).

The nictitating membrane does not enter into the formation of the Brille in the rattlesnake. The normal location of the nictitans in the chick is on the nasal side, in the space between the lids and the eyeball (fig. 18). Schwarz-Karsten found it in a similar location in *Lacerta agilis*, a reptile which possesses both eyelids and nictitans. I was unable to find any evidence of a nictitans in the rattlesnake eye.

COMMENT

The embryonic eye of all vertebrates, from those of the lowest to those of the highest type, is a membranous sac filled with fluid and containing a retina of cerebral origin. The addition of accessory structures to this primitive cystic

eye makes it a marvelous instrument of vision that is seen in the adult organism. The nature and function of these various additional parts were originally determined by the habits and environments of the ancestors of the vertebrates that now possess them. The Brille or spectacle is a secondary feature of the snake's eye.

The characteristics of the Brille anlagen in *Crotalus* make it clear that the fact that the transitory aperture migrates dorsad during its closure is not due to an accident. The lower lid most certainly arises first and makes the major contribution to the definitive structure. Growing as it does from two separate anlagen, the *Crotalus* Brille exhibits a more primitive embryology than does that of *Natrix*, and passes through a phylogenetic stage which *Natrix*, although a member of a less highly specialized family, elides in its own ontogeny.* Even so, the fissure form of the late stage of the aperture in *Crotalus* is open to the interpretation of being primitive, and, furthermore, makes it safe to conclude that the nictitating membrane does not enter into the formation of the Brille. In its structure only the upper and lower lids are involved.

The method of formation of the fissure and its final disposition at the time of closure are interesting subjects for conjecture, but can be determined definitely only by further study of embryos in the various stages of coalescence. If the closure occurs as has been suggested here an interesting result must be the isolation of the epithelial lining of the sulcus and its inclusion in the substance of the Brille itself. A study of the structure of the tissues at each end of the sulcus (fig. 17) suggests a filling in beneath the epithelium in a manner analogous to the method of repair of the defect resulting from a corneal ulcer. Since the process is a develop-

* It is quite possible—in fact, most probable—that still younger *Natrix* embryos than those with which Schwarz-Karsten began his studies would show distinct upper and lower anlagen, and that this author mistook the ringfold for the earliest sign of the Brille formation.

mental one, no trace of the fissure is expected in the adult Brille.

Rochon-Duvigneaud, who has made an extensive study of the eyes of the Reptilia, states: "By a special modification of the eyelids, Ophidians have achieved the protection of their corneas in conditions of permanent menace in which reptation places them, and which necessitates a defense equally permanent."

It is evident that in snakes, whose mode of locomotion is crawling, the eyes would be in constant danger of being injured if it was not for the permanent protection afforded by the insensible covering of the Brille. Examination with the slit-lamp showed its surface to be very highly polished, with a few faint lines or scratches. In addition to the protection afforded against injury, the Brille prevents the absorption of fluids. A 2 per cent. solution of atropin was held on the Brille for five minutes without any effect on the size or reaction of the pupil. A similar test with a 1 per cent. solution of eserine was negative. The transparent spectacle allows the snake to keep its eyes open at all times in order to detect food, friend, or foe. In fact, the advantage of constant vision may possibly have been an actual causative factor in the development of the Brille.

In snakes, the sense of hearing, if present at all, is very poorly developed, hence undisturbed vision is all the more necessary for their well-being.

G. L. Walls¹⁴ states that the nocturnal habit of certain types of active Reptilia, whose movements in dim light are more hazardous to their eyes, is an added factor responsible for the development of the reptilian spectacle, which is found chiefly in reptiles of nocturnal habits, or in groups descended from ancestors having such habits.

What modifications have occurred in the structure and function of the eye and its adnexa on account of the lids having been fused into a transparent convex "glass," completely

sealing off the conjunctival culdesac from the external world? Only a few of the many changes can be briefly mentioned here.

The possible refractive power of both the Brille proper and of its epidermal shield was grossly tested by viewing objects through them. No positive refractive properties of either could be ascertained. It is barely possible that the Brille serves to eliminate astigmatism, just as plain contact lenses do. Since the conjunctival sac is well protected from external substances, conjunctivitis should be very rare, if present at all. Miss Ida C. Mann, in a private communication, states that she has found pus in the subconjunctival sacs of snakes. Personally, I have never seen conjunctivitis in snakes with uninjured eyes. The spectacle—the perfect contact lens—not only prevents external substances from entering the eye, but it precludes the evaporation of tears. The outline of the greatly atrophic tear gland (fig. 12) shows it to have been formerly quite large, but, owing to reduced function, it is now composed of a few isolated patches of glandular cells embedded in connective tissue.

In *Crotalus confluentus* Harder's gland, located chiefly in the orbit, is very well developed, even in the absence of a nictitating membrane. Since the gland is so prominent, and owing to the fact that its secretion reaches the pharynx, Cloquet was probably correct in assuming that its function is to supply mucus to assist in deglutition.

CONCLUSIONS

1. The Brille of the rattlesnake (*Crotalus confluentus lutosus*), unlike that of *Natrix natrix* as described by Schwarz-Karsten, arises from distinct lower and upper anlagen corresponding to the lower and upper eyelids of those reptiles whose eyelids are mobile.
2. The lower anlage appears earlier and grows much faster than the upper.
3. The two anlagen extend circumferentially and merge

to form a ring-like fold whose aperture is eccentric; *i. e.*, shifted dorsally due to the more rapid encroachment of the ventral portion of the fold.

4. The aperture of the developing Brille is not circular, as in *Natrix*, at any time, but is first horizontally ovoid and later approaches closer and closer to the slit form attained at the time of its closure.

5. The foregoing statements lead to the conclusion that the embryology of the Brille in *Crotalus* is more primitive and of more certain phylogenetic significance than the condition described in *Natrix* by Schwarz-Karsten.

6. In snakes the nictitating membrane has entirely disappeared, never having been incorporated into the Brille. Its lubricatory gland (the Harderian) has, however, persisted and become converted into a salivary gland.

7. The final closure of the Brille aperture in *Crotalus* occurs even further dorsad than in *Natrix*—the lower eyelid contributing even more to the Brille than in the latter genus. Just before healing, the lips of the fissure form a “tongue and groove” combination, but the histology of the healing process remains to be worked out.

8. No trace of the fissure of closure is discernible histologically in the adult rattlesnake.

The research work for this paper was done in the Department of Zoology at the University of Utah. Various members of the department rendered valuable assistance. Appreciation is expressed to Dr. Walter P. Cottam, of the Department of Botany, for his assistance in photographing the slides; to Dr. Thomas A. Flood, Pathologist at Holy Cross Hospital, for drawings that bring out greater detail than is possible with the camera; and to Dr. Maurice Gordon, for assistance in translating foreign literature. Special mention is due Dr. G. L. Walls, of the Department of Zoology, State University of Iowa, for his assistance with the bibliography and the methods of embedding, and for advice and inspiration.

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MATHEMATICAL OBSERVATIONS ON JACKSON'S CROSS-CYLINDER IN RELATION TO THE CONOID OF STURM*

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In studying the interval of Sturm it is manifest that we must choose a standard eye which we will assume as the normal. In the literature I have found so many variations in the measurements of so-called normal eyes that I have decided to adopt for this study the one that offers the greatest simplicity in calculation. The reduced eye of Listing¹ seems to fill this requirement, having a posterior focal power of 50 diopters, a posterior focal length of 20 mm., and a nodal point 15 mm. in front of the retina.² We will disregard the effects of the angles alpha, gamma, and kappa, for although they have some effect on the size and shape of the retinal image, such effect would be a constant, and consequently would not influence the relative findings with different lenses; they would serve only to make more intricate the

* Candidate's thesis for membership accepted by the Committee on Theses.